vol. 188, no. 3 the american naturalist september 2016

Natural History Note

Discovery of a Giant Chameleon-Like Lizard (*Anolis*) on Hispaniola and Its Significance to Understanding Replicated Adaptive Radiations

D. Luke Mahler,[1,*] Shea M. Lambert,[2] Anthony J. Geneva,[3] Julienne Ng,[4] S. Blair Hedges,[5] Jonathan B. Losos,[3] and Richard E. Glor[6,†]

1. Department of Ecology and Evolutionary Biology, University of Toronto, Toronto, Ontario M5S 3B2, Canada; 2. Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721; 3. Department of Organismic and Evolutionary Biology and Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138; 4. Department of Ecology and Evolutionary Biology, University of Colorado–Boulder, Boulder, Colorado 80309; 5. Center for Biodiversity, Temple University, Philadelphia, Pennsylvania 19122; 6. Herpetology Division, Biodiversity Institute and Department of Ecology and Evolutionary Biology, University of Kansas, Lawrence, Kansas 66045

Submitted October 28, 2015; Accepted April 11, 2016; Electronically published June 17, 2016

Online enhancements: appendix. *Dryad data:* http://dx.doi.org/10.5061/dryad.sf540.

ZooBank registration: urn:lsid:zoobank.org:pub:42C56F2F-577B-4929-8F5B-6A7251A303D6.

abstract: We report a new chameleon-like *Anolis* species from Hispaniola that is ecomorphologically similar to congeners found only on Cuba. Lizards from both clades possess short limbs and a short tail and utilize relatively narrow perches, leading us to recognize a novel example of ecomorphological matching among islands in the well-known Greater Antillean anole radiation. This discovery supports the hypothesis that the assembly of island faunas can be substantially deterministic and highlights the continued potential for basic discovery to reveal new insights in well-studied groups. Restricted to a threatened band of midelevation transitional forest near the border of the Dominican Republic and Haiti, this new species appears to be highly endangered.

Keywords: community assembly, determinism, conservation, island biogeography, Dominican Republic.

Introduction

Greater Antillean *Anolis* are a well-studied group of lizards, renowned for their tendency to independently evolve highly similar faunas on different islands (Losos 2009). Most Greater Antillean anole species are ecologically and morphologically matched to counterparts occurring on other islands, suggesting that the buildup of island faunas can be deterministic over evolutionary timescales (Losos et al. 1998; Mahler et al. 2013). These matched sets of habitat specialists are called ecomorphs, and each Greater Antillean island is home to between four and six ecomorph classes (Williams 1983; Losos 2009).

However, not all anoles belong to an ecomorph class, and on Cuba and Hispaniola especially, many distinctive species are found that are not ecologically or morphologically similar to species from any other island. For example, Cuba is home to a clade of giant, slow-moving, chameleon-like anoles (the *chamaeleonides* clade); a semiaquatic stream specialist (*Anolis vermiculatus*); and a long-limbed karst specialist (*Anolis bartschi*), none of which are ecomorphologically similar to species from Jamaica, Puerto Rico, or Hispaniola (Leal and Losos 2000; Leal et al. 2002; Losos 2009). It remains unclear why some forms have evolved just once in an otherwise highly replicated system, but island area may be a factor (Gavrilets and Vose 2005). Within the Greater Antilles, the total diversity of morphological forms is higher on larger islands, and this pattern is driven in part by the greater diversity of nonecomorphs on larger islands (Mahler et al. 2013).

In 2007, naturalist Miguel Landestoy discovered a chameleon-like anole in the Dominican Republic that differed greatly from any other species occurring on Hispaniola today. It was, however, similar in general appearance and habits to Cuban anoles from the *chamaeleonides* clade. Through detailed morphological and genetic examination, described below, we confirmed that this is, indeed, a new species. To understand its phylogenetic relationships and ecomorphological affinities to other species both on Hispaniola

* Corresponding author; e-mail: luke.mahler@utoronto.ca.
† ORCIDs: Mahler, http://orcid.org/0000-0001-6483-3667; Geneva, http://orcid.org/0000-0001-8253-6527; Glor, http://orcid.org/0000-0002-3359-1631.

Am. Nat. 2016. Vol. 188, pp. 357–364.
DOI: 10.1086/687566

and elsewhere in the Caribbean, we conducted phylogenetic and morphometric analyses and made natural history observations in the field and in the laboratory. Although most closely related to other Hispaniolan anoles, the new species is most similar to Cuban *chamaeleonides*-clade anoles in morphology and ecology, providing evidence for an additional example of ecomorphological matching among Greater Antillean islands and shedding new light onto patterns of among-island species similarity in a classic replicated adaptive radiation.

Material and Methods

Systematic Account

We base our description on a detailed morphological investigation of preserved specimens; field observations of distribution, habitat use, and behavior; and laboratory observations of behavior and reproduction. For physical descriptions of specimens, we employ characters and terminology described in Williams et al. (1995). Specimens are deposited in the Harvard University Museum of Comparative Zoology (MCZ) and the Museo Nacional de Historia Natural, Santo Domingo (MNHNSD). See the appendix (available online) for additional details.

Phylogenetic Affinities

We sequenced both mitochondrial DNA (mtDNA; one locus) and nuclear DNA (nDNA; nine loci) from three individuals of the new species for use in phylogenetic analyses. To investigate the phylogenetic placement of the new species within *Anolis*, we used Bayesian methods (Huelsenbeck and Ronquist 2001; Drummond and Rambaut 2007) to analyze a partitioned, concatenated alignment of five nDNA loci representing 95 species of *Anolis*, including one individual from the new species. We repeated these analyses including the mtDNA locus ND2 (six loci total). For both sets of analyses, we calculated the posterior probabilities that (1) the new species and the members of the Hispaniolan *ricordii* clade formed a monophyletic group, (2) the new species and the members of the Cuban *chamaeleonides* clade formed a monophyletic group, and (3) the new species, the members of the Hispaniolan *ricordii* clade, and the members of the Cuban *chamaeleonides* clade together formed a monophyletic group.

To further investigate the fine-scale relationships of the new species to its closest Hispaniolan relatives (the three species of the *ricordii* clade), we then conducted species tree analyses (Ané et al. 2007; Heled and Drummond 2010; Larget et al. 2010) using 10 loci (nine nDNA, one mtDNA) on a sample including 62 *ricordii*-clade individuals sampled from 25 localities in the Dominican Republic as well as three individuals of the new species. We also conducted Bayesian phylogenetic analyses (Huelsenbeck and Ronquist 2001) on a concatenated alignment containing these same data, both including and excluding the mtDNA locus ND2.

Ecomorphological Affinities

To quantify the ecomorphological similarity of the new species to other Greater Antillean anoles, we calculated its Euclidean distance to each of 71 other species in a four-dimensional morphospace of traits associated with habitat specialization in anoles, following Mahler et al. (2013). We then tested whether the new species formed a distinct phenotypic cluster with the giant Cuban *chamaeleonides*-clade anoles by conducting a linear discriminant analysis (LDA) with seven categories—one representing the new species plus the members of the *chamaeleonides* clade, and one for each traditional *Anolis* ecomorph. We also conducted preliminary behavioral and habitat use observations of the new species in the wild (see section S1[e] of the appendix).

Results

Systematic Account

Anolis landestoyi sp. nov.

Etymology. The specific epithet is a patronym honoring Dominican naturalist Miguel Landestoy, who discovered the species.

Holotype and Paratypes. Three adult males (holotype: MCZ R-188774; paratypes: MCZ R-188775, MCZ R-188776) and three adult females (paratypes: MCZ R-188777, MCZ R-188778, MCZ R-188779/MNHNSD 23.2979) collected between March 22, 2010, and January 22, 2011, from Reserva Biológica Loma Charco Azul, Independencia Province, Dominican Republic (elevation: 455–526 m), and two juveniles hatched from eggs laid in captivity (male paratype: MCZ R-188780; female paratype: MCZ R-188781).

Diagnosis. A large (snout-to-vent length [SVL]: 122–135 mm for males; 125–133 mm for females), lichenate anole with short limbs and tail, and large bluish dewlap with dark reticulations (figs. 1, 2, S2; figs. S1–S9 are available online). Possesses prominent dark stripe from above eye to corner of mouth and large nuchal ocellus anterior to shoulder (figs. 1, 2, S2, S3). Distinguishable from other large Hispaniolan *Anolis* by lichenate dorsal pattern, eye stripe, nuchal ocellus, dewlap color and pattern, short tail ($<1.35\times$ SVL), short limbs, subocular/supralabial contact, interparietal scale as large as ear or larger, and conspicuously flat, smooth dorsals (figs. 1, 2, S1, S2; tables S2, S3; tables S1–S12 are available

Figure 1: *Anolis landestoyi* sp. nov. (DLM_DR2011_11), posed in natural habitat. Courtesy of Miguel Landestoy.

online). Distinguishable from similar anoles in the Cuban *chamaeleonides* clade by dewlap color and pattern; absence of a large, rugose parietal casque in adults; presence of nuchal ocellus; presence of a single scale between nasal and rostral, flank scales in partial contact; weakly to strongly keeled ventrals; and multicarinate supradigitals (table S3). Additional diagnostic information is provided in section S1(c) of the appendix and table S3.

Description. A large-bodied *Anolis* (SVL: 122–135 mm); tail short (150–178 mm); males and females morphologically similar; head moderately elongated; body slightly laterally compressed; dewlap large; anterior head scales large, irregular, pyramidal; ridges of 5–7 enlarged, blocky canthals meet 1–3 elongate, keel-shaped, enlarged supraciliaries posteriorly; longitudinal nasal ridges between canthals separated by shallow medial depression; 7–9 scales between second canthals; supraorbital semicircles enlarged, separated by 2–3 scales; interparietal elongate, larger than adjacent scales, separated from supraorbital semicircles by 3–5 scales; suboculars somewhat rugose, modestly keeled, directly contacting supralabials; loreals, labials, and sublabials large, well differentiated, and flat compared with dorsal cranial scales; loreals in 5–7 loose rows; chin and eyelid scales small, granular, arranged loosely into longitudinal rows; 6–8 postmentals; nasals circumnasal, often with anteroventral suture; mental half-divided; ear vertically ovular with enlarged dorsal margin scales, similar in size to interparietal; dorsals irregular, nonimbricate, flat, smooth, circular or subrectangular, mostly large; those near dorsal crest weakly unicarinate; nuchal/dorsal crest with single row enlarged, laterally flattened, triangular scales from head to base of tail; crest skin loose, folded, with scales sometimes slightly larger than adjacent dorsals; ventrals regular, subimbricate, keeled, slightly mucronate, smaller toward midline; dorsal limb scales keeled, imbricate, arranged into regular diagonal rows; ventral limb scales nonimbricate (or subimbricate), circular, less regular; supradigitals multicarinate; adhesive subdigital pads well developed; claws tall, robust proximally, recurved distally; males have two large subrectangular postanal scales; hemipenes stout, weakly bilobed, symmetrical; pedicel naked, with transverse folds where it meets lobes; small calyces cover lobes; sulcus spermaticus reaches apical nude patch spanning lobes (fig. S5); tail laterally compressed, blunt-tipped.

In life, dorsum greenish gray and light brown with irregular black and brown blotches; ventrum white with char-

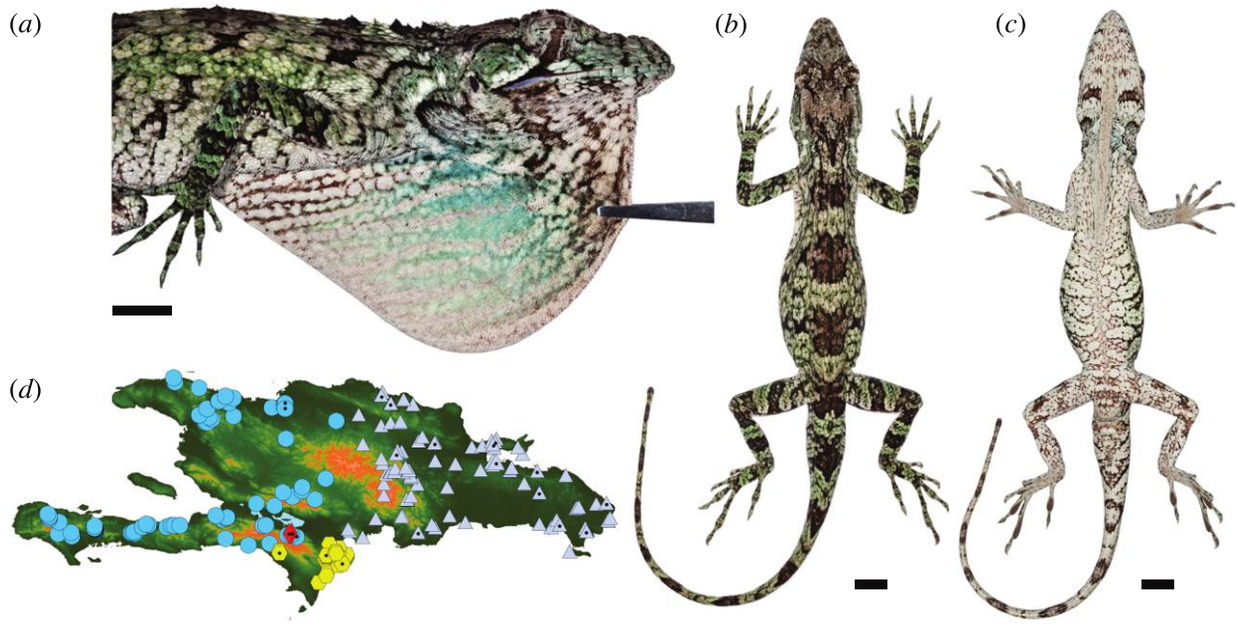

Figure 2: *a–c*, *Anolis landestoyi* sp. nov. holotype in life (MCZ R-188774; scale bars = 10 mm). *a*, Right lateral profile. *b*, Dorsal view (photoreversed). *c*, Ventral view. *d*, Distributions of giant Hispaniolan anole species (red diamonds = *A. landestoyi*; yellow hexagons = *A. barahonae*; pale blue triangles = *A. baleatus*; blue circles = *A. ricordii*). Points indicate sampled localities.

coal reticulations; dark diagonal streak from above eye to corner of mouth; iris dark brown with cream-colored inner ring (fig. S3*a*); dewlap sky blue, fading to light sea green distally, with indistinct longitudinal rows of whitish gorgetals; dewlap often with several diffuse concentric charcoal rings; female dewlap slightly smaller, less intensely blue (fig. S2*a*); tongue, lining of mouth pinkish (fig. S3*c*).

Found in midelevation (455–526 m) transition zone between dry forest and upland rain forest, with abundant Spanish moss and epiphytic lichens (fig. S6*a*, S6*b*). Diurnal, secretive, slow moving, arboreal; uses relatively narrow perches (1.5–2.5 cm) in cluttered arboreal habitats; primarily crawls or walks, although occasionally runs or jumps; diet includes various arthropods; displays involve push-ups and protracted dewlap extensions punctuated by several rapid retractions and extensions; may erect prominent dorsal crest.

An expanded account can be found in section S1 of the appendix.

Phylogenetic Affinities

Bayesian phylogenetic analyses of 95 *Anolis* species consistently supported a monophyletic group including *A. landestoyi* and the three members of the Hispaniolan *ricordii* clade of "crown-giant" anoles (posterior probability [pp] = 1.0 in five- and six-locus analyses), while none supported a monophyletic group composed of *A. landestoyi* and the members of the Cuban *chamaeleonides* clade (pp = 0.0 in both analyses). For the five-locus nDNA analyses, a significant minority of trees in the posterior distribution (pp = 0.18) indicated a sister relationship between the *chamaeleonides* and *ricordii* clades (with the latter including *A. landestoyi*), although for most trees these clades were separated by *A. christophei* (pp = 0.24), *A. eugenegrahami* (pp = 0.01), or both (pp = 0.57). For the six-locus analyses including mtDNA, the *chamaeleonides* and *ricordii* clades were never sisters and were always separated by both *A. christophei* and *A. eugenegrahami* (pp = 1.0).

Despite consistent support for a relationship between *A. landestoyi* and the members of the *ricordii* clade, analyses of five nDNA loci recovered *A. landestoyi* as sister to the three-species *ricordii* crown clade with strong support (fig. S7*a*), while the six-locus analyses including mtDNA found *A. landestoyi* nested within this clade. We conducted species tree analyses to investigate this conflict.

Species tree analyses of 10 loci (nine nDNA, one mtDNA) from 65 individuals—as well as partitioned analyses of a concatenated nDNA-only data set—consistently recovered *A. landestoyi* as sister to the three species in the *ricordii* clade (figs. S7*b*, S7*c*, S8*a*). When the mitochondrial locus ND2 was included in concatenated analyses, *A. landestoyi* was inferred as sister to nearby populations of *A. ricordii*, rendering *A. ricordii* paraphyletic (fig. S8*b*). The close geographic prox-

imity (<2 km) of the *A. ricordii* and *A. landestoyi* localities in question suggests that mtDNA introgression can explain this cytonuclear discordance, as incomplete lineage sorting is not expected to leave predictable geographic patterns and resolves more quickly in mitochondrial versus nuclear markers (Funk and Omland 2003).

Ecomorphological Affinities

Although most closely related to other giant Hispaniolan anoles, comparative analyses of 11 continuous traits associated with anole habitat specialization sampled from 72 Greater Antillean species reveal *A. landestoyi* to be most similar to Cuban *chamaeleonides*-clade anoles (figs. 3, S9; table S5). These species cluster together in morphospace as closely as members of the six traditional Greater Antillean ecomorphs (Losos 2009). In an LDA including six ecomorph categories plus a seventh category containing *A. landestoyi* plus the *chamaeleonides* clade, species in the latter group were correctly classified with high probability (table S6). We tentatively designate this group the "twig-giant" ecomorph, following informal terminology used by Hass et al. (1993) to refer to members of the *chamaeleonides* clade. Preliminary observations suggest that *A. landestoyi* also matches *chamaeleonides*-clade species in ecology and behavior, including its tendency to move slowly and use narrow perches (see section S1[e] of the appendix).

Discussion

Anolis landestoyi is conspicuously distinct from any other species of anole from Hispaniola, but it is very similar to a clade of giant cryptic anoles found only on Cuba. The discovery of a new example of ecomorphological matching between Hispaniolan and Cuban anoles contributes two insights to current thinking about faunal assembly in replicated island radiations. First, *A. landestoyi* strengthens the pattern of among-island faunal similarity for which Greater Antillean anoles are well known. Previously, the Cuban *chamaeleonides* clade was regarded as an ecological, morphological, and evolutionary singleton because it arose once and is restricted to a single island (Losos 2009). We show here that it has an ecomorphological counterpart on Hispaniola.

A second insight derives from the fact that *A. landestoyi* and the *chamaeleonides* clade occur only on the largest pair of Caribbean islands: Hispaniola and Cuba. In the Greater Antilles, there is a positive relationship between island area and the morphological diversity of the anole fauna, and this relationship is due to the fact that larger islands contain both more types of ecomorphs (Cuba and Hispaniola have six, Puerto Rico five, and Jamaica four) as well as greater numbers of nonecomorph anole species (Losos 2009; Mahler et al. 2013). An additional ecomorphological match between *A. landestoyi* and the *chamaeleonides* clade on the largest two Greater Antilles strengthens the deterministic component of an area-diversity relationship that previously had been largely attributed to the greater diversity of nonecomorph forms on larger islands (Mahler et al. 2013).

While *A. landestoyi* and Cuban *chamaeleonides*-clade anoles represent among-island ecomorphological analogues, we are presently unable to ascertain whether their striking similarity is due to homology or convergence and, thus, whether the twig-giant grouping represents a new *Anolis* ecomorph in the strict sense of the term. In defining the ecomorph concept, Williams (1972, 1983) included evolutionary convergence as an important criterion. For a group of species to qualify as an ecomorph, it must include species that had independently evolved the same morphology, ecology, and behavior.

Williams's distinction is an important one because it is possible for communities to be composed of similar habitat specialists simply because representatives of the same clades are present in each place. Such a situation could occur if adaptive radiation occurred on one island and then each of the habitat specialists colonized other islands. Adaptive radiation followed by vicariance could produce the same result. In both cases, adaptive radiation would not be replicated, and the similarity in faunas among islands would not be the result of convergence.

In Greater Antillean anoles, among-island similarity can mostly be attributed to convergence (Mahler et al. 2013), although there is at least one very likely case of among-island matching due to colonization (the *sheplani* clade of Hispaniolan twig anoles nests phylogenetically within a larger clade of Cuban twig and trunk-crown anoles). We cannot yet determine whether the striking similarity of *A. landestoyi* and Cuban *chamaeleonides*-clade anoles is due to homology or convergence. While the two groups are not sisters in most of the phylogenies in the Bayesian posterior distribution, they did occupy adjacent branches in a substantial minority of these trees (18%), leaving open the possibility that the similar features of these taxa have a single evolutionary origin. Furthermore, even if not sister taxa, the twig-giant anoles share a relatively recent common ancestor, which means that phylogenetic information alone cannot resolve whether their similarity results from convergence or shared ancestry. The latter scenario would require independent divergence from this morphology in the one or two phylogenetically intermediate lineages inferred in the Bayesian posterior distribution (i.e., *A. eugenegrahami* and *A. christophei*, or a single clade containing both of these species; fig. 3*d*). We regard both scenarios as inherently plausible. If *A. landestoyi* and the *chamaeleonides* clade are similar because of shared ancestry, this would represent one of very few cases in which descendants of the same ecomorphological lineage are found on multiple Greater

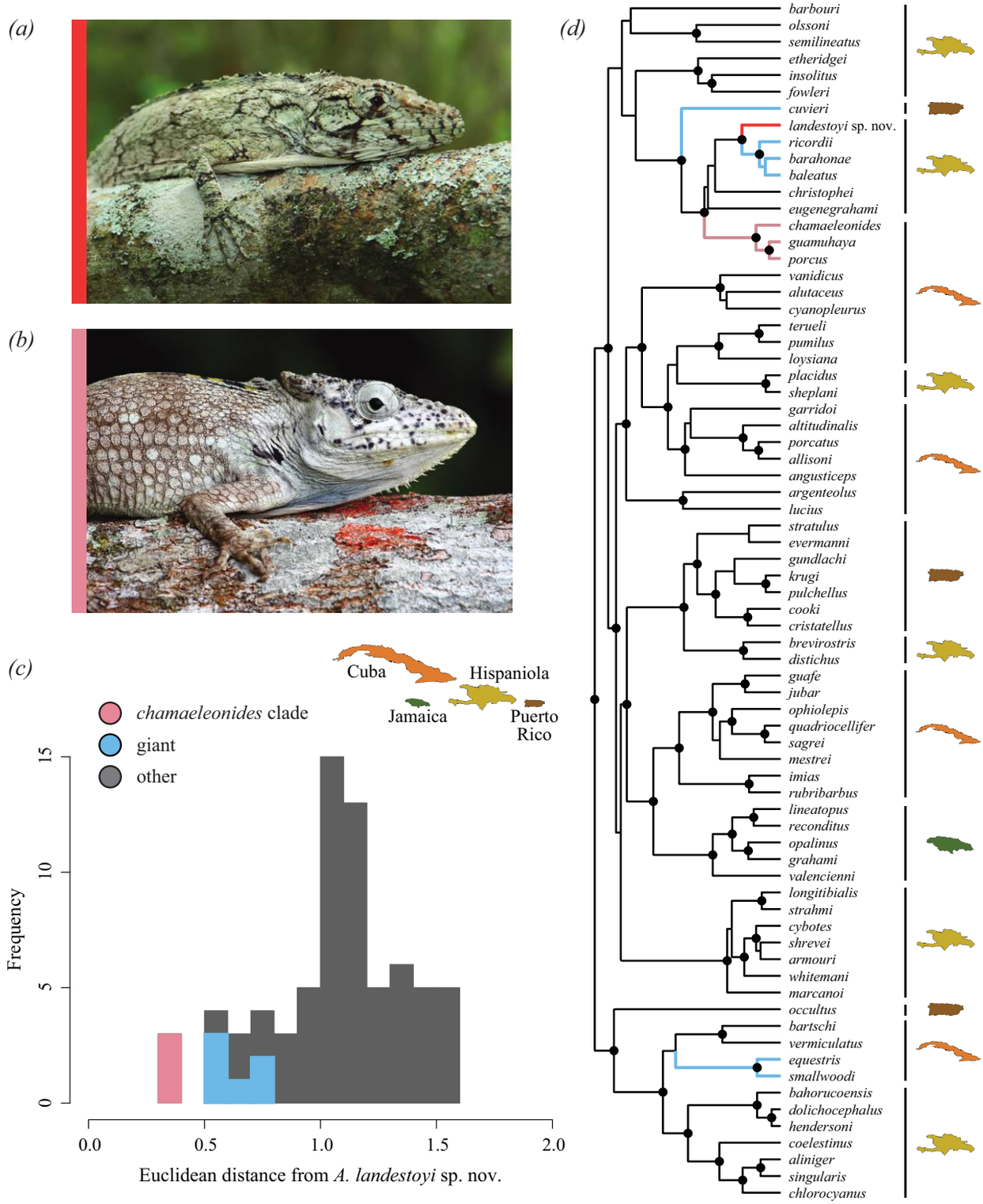

Figure 3: *Anolis landestoyi* sp. nov. is most ecomorphologically similar to Cuban *chamaeleonides*-clade anoles, but these clades likely are not sisters. *a*, *Anolis landestoyi*. *b*, *Anolis porcus*, a *chamaeleonides*-clade representative. *c*, Distribution of Euclidean morphospace distances between *A. landestoyi* and other Greater Antillean *Anolis*. *d*, Maximum clade credibility chronogram of Greater Antillean anole diversification from a partitioned BEAST analysis of nuclear DNA. Nodes with posterior probabilities of 0.95 or higher are indicated by black dots. Colors represent crown-giant anoles (blue), Cuban twig-giant anoles (pink), and Hispaniolan *A. landestoyi* (red). Geographic locations of species are indicated by island silhouettes to the right of the phylogeny (island key is to the left). Photos in *a* and *b* are courtesy of Miguel Landestoy.

Antillean islands, as well as one of the few cases in *Anolis* in which one type of ecological specialist is paraphyletic with respect to another (in this case, a clade of crown-giant anoles arising within a clade of twig-giant anoles).

Anolis landestoyi is known only from Loma Charco Azul, a scientific reserve established in 2009 to protect an unusual habitat that is home to several endangered Hispaniola-endemic species, such as the solenodon (*Solenodon paradoxus*), Ricord's iguana (*Cyclura ricordii*), and the bay-breasted cuckoo (*Coccyzus rufigularis*; fig. 2*d*; León et al. 2011). Nonetheless, this reserve continues to be degraded by illegal clear-cutting for agriculture, livestock grazing, and firewood (fig. S6*c*, S6*d*). Given the ongoing and projected degradation of its only known habitat, we suggest that *A. landestoyi* be classified as Critically Endangered according to International Union for Conservation of Nature criteria (CR B1ab(iii)).

It is commonly assumed that the age of discovery for strikingly distinct new species of vertebrates has largely passed, especially in well-studied regions like the Greater Antilles. Our discovery of a large *Anolis* lizard on the relatively well-surveyed island of Hispaniola challenges this view and joins other recent findings to demonstrate the continued scientific importance of species discovery (Reeder et al. 2007). Recent vertebrate discoveries have added long branches to the tree of life (Johnson et al. 2011), uncovered living representatives of fossil families (Dawson et al. 2006), and provided new evidence for biogeographic connections (Min et al. 2005; Lundberg et al. 2007; Welton et al. 2010). Likewise, the discovery of *A. landestoyi* provides new insight into deterministic faunal assembly in adaptive radiations.

Data Accessibility

DNA sequences generated for this work have been deposited in GenBank (KU979015–KU980143). Archived data, including a spreadsheet with GenBank numbers and specimen voucher information, are available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.sf540 (Mahler et al. 2016).

Acknowledgments

For loans, assistance, and constructive comments, we thank C. Boccia, J. Brocca, R. Brown, C. Davis, K. de Queiroz, K. Helgen, Y. Hernandez, F. Jenkins, M. Landestoy and family, A. Marmolejo, C. Marte, J. Martinez, T. Mejia, L. Meszoly, M. Muñoz, N. Navarro, S. Poe, R. Powell, M. Quírico, J. Rosado, D. Scantlebury, M. Stimola, T. Takahashi, R. Thomas, L. Vitt, C. Wessinger, and one anonymous reviewer. Research permission was granted by the Ministerio de Medio Ambiente y Recursos Naturales, Dominican Republic (permits 2009-0001179, 2010-0000818). Support was provided by the National Science Foundation (DEB-0918975, DEB-0808401) and Harvard University's David Rockefeller Center for Latin American Studies.

Literature Cited

Ané, C., B. Larget, D. A. Baum, S. D. Smith, and A. Rokas. 2007. Bayesian estimation of concordance among gene trees. Molecular Biology and Evolution 24:412–426.

Dawson, M. R., L. Marivaux, C. Li, K. C. Beard, and G. Métais. 2006. *Laonastes* and the "Lazarus effect" in Recent mammals. Science 311: 1456–1458.

Drummond, A. J., and A. Rambaut. 2007. BEAST: Bayesian evolutionary analysis by sampling trees. BMC Evolutionary Biology 7: 214.

Funk, D. J., and K. E. Omland. 2003. Species-level paraphyly and polyphyly: frequency, causes, and consequences, with insights from animal mitochondrial DNA. Annual Review of Ecology, Evolution, and Systematics 34:397–423.

Gavrilets, S., and A. Vose. 2005. Dynamic patterns of adaptive radiation. Proceedings of the National Academy of Sciences of the USA 102:18040–18045.

Hass, C. A., S. B. Hedges, and L. R. Maxson. 1993. Molecular insights into the relationships and biogeography of West Indian anoline lizards. Biochemical Systematics and Ecology 21:97–114.

Heled, J., and A. J. Drummond. 2010. Bayesian inference of species trees from multilocus data. Molecular Biology and Evolution 27: 570–580.

Huelsenbeck, J. P., and F. Ronquist. 2001. MRBAYES: Bayesian inference of phylogenetic trees. Bioinformatics 17:754–755.

Johnson, G. D., H. Ida, J. Sakaue, T. Sado, T. Asahida, and M. Miya. 2011. A "living fossil" eel (Anguilliformes: Protoanguillidae, fam. nov.) from an undersea cave in Palau. Proceedings of the Royal Society B: Biological Sciences 279:934–943.

Larget, B. R., S. K. Kotha, C. N. Dewey, and C. Ané. 2010. BUCKy: gene tree/species tree reconciliation with Bayesian concordance analysis. Bioinformatics 26:2910–2911.

Leal, M., A. K. Knox, and J. B. Losos. 2002. Lack of convergence in aquatic *Anolis* lizards. Evolution 56:785–791.

Leal, M., and J. B. Losos. 2000. Behavior and ecology of the Cuban "chipojos bobos" *Chamaeleolis barbatus* and *C. porcus*. Journal of Herpetology 34:318–322.

León, Y. M., E. Rupp, Y. Arias, L. Perdomo, S. J. Incháustegui, and E. Garrido. 2011. Estrategia de monitoreo para especies amenazadas de la Reserva de Biosfera Enriquillo-Bahoruco-Jaragua. Grupo Jaragua, Santo Domingo.

Losos, J. B. 2009. Lizards in an evolutionary tree: ecology and adaptive radiation of anoles. University of California Press, Berkeley.

Losos, J. B., T. R. Jackman, A. Larson, K. de Queiroz, and L. Rodríguez-Schettino. 1998. Contingency and determinism in replicated adaptive radiations of island lizards. Science 279:2115–2118.

Lundberg, J. G., J. P. Sullivan, R. Rodiles-Hernández, and D. A. Hendrickson. 2007. Discovery of African roots for the Mesoamerican Chiapas catfish, *Lacantunia enigmatica*, requires an ancient intercontinental passage. Proceedings of the Academy of Natural Sciences of Philadelphia 156:39–53.

Mahler, D. L., T. Ingram, L. J. Revell, and J. B. Losos. 2013. Exceptional convergence on the macroevolutionary landscape in island lizard radiations. Science 341:292–295.

Mahler, D. L., S. M. Lambert, A. J. Geneva, J. Ng, S. B. Hedges, J. B. Losos, and R. E. Glor. 2016. Data from: Discovery of a giant chameleon-like lizard (*Anolis*) on Hispaniola and its significance to understanding replicated adaptive radiations. American Naturalist, Dryad Digital Repository, http://dx.doi.org/10.5061/dryad.sf540.

Min, M. S., S. Y. Yang, R. M. Bonett, D. R. Vieites, R. A. Brandon, and D. B. Wake. 2005. Discovery of the first Asian plethodontid salamander. Nature 435:87–90.

Reeder, D. M., K. M. Helgen, and D. E. Wilson. 2007. Global trends and biases in new mammal species discoveries. Occasional Papers, Museum of Texas Tech University 269:1–35.

Welton, L. J., C. D. Siler, D. Bennett, A. Diesmos, M. R. Duya, R. Dugay, E. L. B. Rico, et al. 2010. A spectacular new Philippine monitor lizard reveals a hidden biogeographic boundary and a novel flagship species for conservation. Biology Letters 6:654–658.

Williams, E. E. 1972. The origin of faunas. Evolution of lizard congeners in a complex island fauna: a trial analysis. Evolutionary Biology 6:47–89.

———. 1983. Ecomorphs, faunas, island size, and diverse end points in island radiations of *Anolis*. Pages 326–370 *in* R. B. Huey, E. R. Pianka, and T. W. Schoener, eds. Lizard ecology: studies of a model organism. Harvard University Press, Cambridge, MA.

Williams, E. E., H. Rand, A. S. Rand, and R. J. O'Hara. 1995. A computer approach to the comparison and identification of species in difficult taxonomic groups. Breviora 502:1–47.

Natural History Editor: Mark A. McPeek

Anolis landestoyi perched on a branch. Photo courtesy of Miguel Landestoy.